

Homing Behaviour and Population Regulation in the Limpet *Acmaea (Collisella) digitalis*

BY

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INTRODUCTION

LIMPETS THAT ARE EXPOSED to air during part of the tidal cycle usually remain immobile during that period. In several species of *Acmaea*, limpets are reported to return to a home site in which they remain at low tide (WELLS, 1917). Such behaviour may assure the limpet protection from desiccation.

Several authors have studied homing behaviour in *Acmaea digitalis* Rathke, 1833, which lives high in the intertidal zone of exposed rocky shores on the Pacific coast. FRANK (1964) found that marked individuals remained within small areas for long periods of time, and termed such a small area a "home range." Although FRANK (1965) reported that strict homing does not occur, MILLER (1968) found that 25% of the limpets he observed showed a tendency to return to a home site. GALBRAITH (1965) found that 54% homing occurred in 26 *A. digitalis* watched for 7 days. MILLARD (1968), studying the behaviour by which *A. digitalis* forms aggregations or "clumps," reported that half the original limpets of a clump remained within the clump after a month. Different procedures were used by each of these authors to study homing, which might partially account for differences among their results.

It is of interest that some individuals in the studies cited above show homing behaviour while others do not. FRANK (1965) suggests that homing may be a response to favourable local conditions: "Behaviour evidently is also involved in regulating abundance, probably in an interaction with space and food. As long as their preferred habitat is not saturated, limpets tend to remain where they are." He also found that when limpets were artificially crowded on a part of the shore, emigration from that part was increased. This indicates that individuals may respond to less favourable local conditions by ceasing to home, thus tending to migrate away.

FRANK (1965) further suggests that differences among individual tolerances of local conditions might buffer such a system of local regulation of density. At any level of density, and hence at any level of local conditions, some limpets would be tolerant, and would show homing; others would be intolerant, and so would not show homing. Deterioration of conditions would result in a higher proportion of non-homing limpets, and this might tend to reduce local density.

A similar hypothesis is suggested by LOMNICKI (1969), who found that land snails, *Helix pomatia* Linnaeus, 1758, can be divided into 2 groups. Some snails are quite mobile and are usually found on the surface; others are less mobile and are usually beneath the surface. Lomnicki suggests that the more mobile snails are the "excess" in relation to local resources. An increase in the proportion of mobile snails might tend to reduce local density to the level which can be supported by the habitat.

The purpose of this study was to examine the hypothesis that local regulation of density can occur through changes in homing behaviour of *Acmaea digitalis*. The study was carried out in several stages near Port Renfrew, on the west coast of Vancouver Island.

OCCURRENCE OF HOMING

To determine whether homing was demonstrated by individual *Acmaea digitalis* at Port Renfrew, 40 limpets within a small area were individually marked in May, 1969. Small printed numbers on adhesive plastic were obtained from the W. H. Brady Co., which manufactures them for use in marking electrical components. A number was placed on the posterior dorsal portion of the shell and covered with 2 coats of an acrylic resin known as "Dekophane." The original position of each limpet was recorded on a sketch map of the area, and its position was again recorded on 11 subsequent days at low tide.

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Twenty-six limpets were seen in their original location at every observation, 5 changed position once and 9 changed position more than once. Limpets which did not change position appeared to have moved away and returned during high tide, because 22 of these limpets were in small clumps of up to 10 animals, and the relative positions of limpets within these clumps changed.

It was not possible to observe the marked limpets during their feeding periods away from the homesite. When observations were made underwater during day-time high tides, all the limpets were seen in their shelter sites. Feeding presumably occurred during night high tides, when it was not possible to make observations.

It is not possible to test homing in *Acmaea digitalis* by removing a limpet from its shelter site, placing it nearby and observing whether it subsequently returns. It is shown below (Table 10) that a high proportion of limpets that were removed from their sites and immediately replaced in the site migrated away. Removal appears to cause a disturbance which destroys, temporarily at least, the homing behaviour.

It was concluded that homing behaviour is demonstrated by some individual *Acmaea digitalis* at this location.

IDENTIFICATION OF TWO BEHAVIORAL TYPES

The hypothesis which was being tested predicted that 2 types of limpets would be found: namely those that were tolerant of local conditions and showed homing, and those that were intolerant and did not show homing.

Two large samples, each of which comprised all the limpets found within a defined area, were marked individually as described above. On each area a grid system was established so that positions of individuals could be described. On the first area, 28 grid squares were marked on the rock by drilling holes 20 cm apart. On the second area, all limpets were found in 30 small depressions in the rock, in which clumps were formed. These depressions were numbered and used to describe positions of individual limpets.

Each sample was observed for 6 consecutive days. Each day's observation included the location at which each limpet was found and the number of limpets with which it was clumped. A clump was defined as 4 or more limpets grouped in such a way that none was farther than 2 cm from another.

To avoid confusion between changes in shelter position, as seen between successive days at low tide, and feeding movements, the term "migration" was adopted to describe

the former. A limpet which moved from its shelter site to feed and returned to the same site had not migrated; a limpet that adopted a new shelter site had migrated. Migration could occur in 2 ways: a limpet could migrate to a new grid location, or it could migrate from within an established clump within a grid location to a position outside the clump in the same location.

The number of migrations made by each limpet was determined and a distribution of migration frequencies compiled for each sample. These are seen in Tables 1 and 2 for the first and second samples respectively. In both samples, there were more limpets that did not migrate at

Table 1

A comparison between the number of limpets in each category of migration frequency and the expected Poisson distribution, which was calculated from the mean number of migrations per limpet per day. These data were obtained from the first sample of marked limpets, from June 5 through June 10, 1969

Number of migrations	Number of limpets observed	Number of limpets expected
0	56	49.28
1	19	28.53
2	8	8.26
3	4	1.59
4	1	0.23
5	0	0.03
Total	88	87.92

X^2 in the test for Goodness of Fit = 4.94; significant at $\alpha = 0.05$, d. f. = 1.

Table 2

The number of limpets in each category of migration frequency, and the expected Poisson distribution. These data were obtained from the second sample of marked limpets, from August 11 through August 16, 1969

Number of migrations	Number of limpets observed	Number of limpets expected
0	173	145.45
1	24	61.49
2	16	13.02
3	2	1.82
4	4	0.19
5	3	0.02
Total	222	221.99

X^2 in the test for Goodness of Fit = 15.22; significant at $\alpha = 0.001$, d. f. = 1.

all than in any other category, and there were progressively fewer limpets in each category of higher migration frequency.

If all limpets were equally likely to migrate on a given night, and if the probability of any limpet migrating were not affected by whether or not it had migrated on previous nights, then the distribution of migration frequencies would follow a Poisson distribution. This situation might occur if migrations were caused by local, random stimuli, or if limpets had an innate tendency to migrate at random intervals. In such a situation, the pattern of migrations would have little importance with respect to local regulation of density. If the observed distribution of migration frequencies were not in accord with the Poisson distribution, however, it would indicate that limpets were not all equally likely to migrate, or that previous migrations altered the probability of a limpet migrating on a given night.

Table 3

The numbers of limpets in each category of migration frequency. These data were collected during the periods indicated below, from the first sample of marked limpets in 1970

Number of migrations	Number of limpets observed				
	Feb. 15 to Feb. 19	Apr. 29 to May 2	June 1 to June 5	June 16 to June 19	July 23 to July 27
0	35	72	63	73	76
1	9	15	6	6	19
2	5	10	11	11	12
3	1	3	5	5	7
4	1	0	0	0	0
Total	51	100	85	95	114
X ²	4.50	12.05	26.63	29.91	13.90

The observed distributions were compared with the expected Poisson distributions by means of the Chi squared (χ^2) test for Goodness of Fit. These comparisons are also shown in Tables 1 and 2. Both observed distributions were significantly different from the Poisson in the same way. More limpets than expected did not migrate at all, fewer than expected migrated only once and more than expected migrated more than once. In 1970, observation of the first marked sample was continued in an experiment to be discussed below. Five further sets of similar observations were obtained (Table 3). These all show a similar pattern of deviation from the Poisson.

Although these results were in agreement with the prediction made from the hypothesis being tested, namely that a tendency toward two behavioural types would be found, there were alternate possible explanations for the results. If the migration behaviour of small limpets differed from that of large limpets, deviation from the Poisson might occur. This idea was discounted immediately because all limpets on the first area were approximately the same size: between 1.50 and 2.00 cm.

Second, if limpets found in small clumps behaved differently from those in larger clumps, this might also produce the observed deviation from the Poisson. This was tested in each sample by making an arbitrary division between "large" and "small" clumps, so that roughly half the limpets fell into each category. The data were divided according to the size of the clump in which each limpet was initially found. The distributions of migration frequencies from large and small clumps were then compared in each sample by means of the χ^2 test for independence of samples. These comparisons are shown in Tables 4 and 5. In neither sample was there a significant difference between the two distributions of migration frequencies.

Table 4

A comparison between the migration frequency distributions of limpets initially found in large (10 or more limpets) and small (less than 10 limpets) clumps. These data were obtained from the first sample of marked limpets, from July 23 through July 27, 1970

Number of migrations	Small Clumps		Large Clumps	
	Number of limpets observed	Number of limpets expected	Number of limpets observed	Number of limpets expected
0	38	42.67	38	33.33
1	12	10.67	7	8.33
2	8	6.74	4	5.26
3	6	3.93	1	3.07
Total	64	64.01	50	49.99

χ^2 in the test for independence of samples = 3.73; not significant at $\alpha = 0.05$, d. f. = 1.

A third possibility was that the period of observation was too short. The probability that a limpet would migrate on a given night might be altered by whether or not it had migrated in the previous few days, but such bursts of migration activity might still be independent of activity

Table 5

A comparison between the migration frequency distributions of limpets initially found in large (15 or more limpets) and small (less than 15 limpets) clumps. These data were obtained from the second sample of marked limpets, from August 11 through August 16, 1969

Number of migrations	Small Clumps		Large Clumps	
	Number of limpets observed	Number of limpets expected	Number of limpets observed	Number of limpets expected
0	61	61.56	112	111.44
1	8	8.54	16	15.46
2	6	5.70	10	10.31
3	1	0.71	1	1.29
4	2	1.42	2	1.93
5	1	1.07	2	1.93
Total	79	79.00	143	142.36

X^2 in test for independence of samples = 0.39; not significant at $\alpha = 0.05$, d. f. = 1.

a month previously. In this case, migration could be considered independent over the longer term, and observed deviation from the Poisson would have little importance. This possibility was tested by examining the data presented above in Table 3. These data were collected at intervals over 6 months, and the total number of observed

Table 6

The number of limpets in each category of migration frequency, and the expected Poisson distribution. These data have been combined from Table 3

Number of migrations	Number of limpets observed	Number of limpets expected
0	16	6.95
1	8	12.18
2	3	10.65
3	2	6.22
4	4	2.72
5	3	0.95
6	2	0.28
7	2	0.07
Total	40	40.02

X^2 in the test for Goodness of Fit = 33.69; significant at $\alpha = 0.001$, d. f. = 3.

migrations of 40 limpets could be determined. The resulting frequency distribution, which contained 15 possible migration categories, was compared with the Poisson (Table 6). This distribution was not in accord with the Poisson, and the pattern of deviation was similar to that seen in the component sets of observations.

Thus there appeared to be 2 behavioural types of limpets. Some tended not to migrate at all, while others tended to migrate many times. Fewer limpets than expected migrated only once during periods of observation. This behaviour appeared consistent over long periods of time, and could not be explained by differences in behaviour associated with size or clump size. It was concluded that 2 behavioural types of limpets, homing and non-homing, had been detected. This supported the hypothesis which was being tested in this study.

RELATION BETWEEN DENSITY AND HOMING BEHAVIOR

If homing were a response to favourable local conditions, and non-homing to unfavourable conditions, then the proportion of non-homing limpets would be expected to increase if local conditions deteriorated. It was reasoned that increased density within an enclosed area would result in less favourable local conditions within the area, and thus a positive correlation between the percentage of non-homing limpets and density was predicted.

In February, 1970 the area containing the first sample of marked limpets was enclosed with a fence made from plastic mesh. The mesh was fastened to the rock with screws, and the lower edge sealed with a mixture of fibreglass resin, sand and catalyst. All limpets within the fence were marked or remarked. Two sets of observations were made on the migration behaviour of the marked limpets at this natural density. Then limpets from elsewhere were added to the area, increasing density to twice its previous level; and 2 more sets of observations were made. More limpets were added, increasing density to 4 times its original level, and one further set of observations was made.

Only the data obtained from those limpets originally present in the enclosure in February are presented. It was found that limpets which were added to increase the density within the enclosure had a significantly higher rate of migration than the original limpets, so these data were not used. A similar observation was made by LOMNICKI (1969), who reported that snails that he added to his study area behaved like the more mobile snail type.

The percentage of limpets that migrated and the mean number of migrations per limpet per day were calculated during each set of observations, and are presented in Table 7. The correlation between relative density (calculated by dividing the number of limpets in the enclosure by the original number in February) and the percentage migrating was $r = 0.349$. The correlation between relative density and mean number of migrations per limpet per day was $r = 0.242$. Neither was statistically significant, which indicated that there was no relation between density and these two measures of migration rate, at least within the experimental range of densities.

Table 7

Comparison between relative density and percentage of limpets that migrated during the period of observation, and between density and the mean number of migrations per limpet per day

Period of observation	Total number limpets	Relative density	Percentage marked limpets	Mean number migrations/limpet/day
Feb. 15 to Feb. 19	133	1.00	31.4	0.127
April 29 to May 2	125	0.94	28.0	0.146
June 1 to June 5	290	2.18	23.2	0.113
June 16 to June 19	283	2.13	28.2	0.162
July 23 to July 27	561	4.22	33.3	0.149

The results from this experiment thus seem to contradict the hypothesis that local densities can be regulated through changes in homing behaviour. A possible criticism of this experiment, however, is that density was progressively increased from early spring to summer. Changes in seasonal conditions may have caused changes in homing behaviour which compensated for the effect of increasing density. From an experiment carried out during the summer of 1969, which will be presented in a subsequent publication, there is evidence that limpets are more conservative in their movements during summer, when warm, dry weather presents dangers in the form of desiccation. Because seasonal conditions may have affected the outcome, this experiment may not have been an adequate test of the hypothesis.

HOMING

AND

LOCAL ENVIRONMENTAL CONDITIONS

In the previous experiment it was assumed that increased density would result in less favourable local conditions for the limpets; increased density might be expected to cause decrease in the availability of food and space. The following experiments were carried out to determine whether the proportion of non-homing limpets would increase when food and space were decreased directly.

Food availability was decreased directly in two experiments, one in 1969 and one in 1970. In these experiments, algae on the rock surrounding a clump of limpets (marked with quick-drying paint) were removed with a wire brush to a distance of 60 cm from the clump. The number of marked limpets which emigrated from the clump was used as a measure of non-homing, and was compared with the number of emigrants from a control clump, around which the algae had not been removed.

In each experiment the experimental and control clumps were chosen in areas of similar local topography, just far enough apart that movement of limpets from one to the other would be unlikely. For each clump, the number of marked animals remaining in the clump, the number of emigrants and the distances travelled were recorded. The results from the 1969 and 1970 experiments are presented in Tables 8 and 9 respectively. The number of emigrants from the experimental clump was

Table 8

The number of limpets remaining, the number of emigrants and the median distance travelled by emigrants in the experimental (E) and control (C) groups of an experiment designed to measure the response of limpets to reduced food levels. Algae were removed from around the experimental group on July 30, August 2, 10, 15 and September 1, 1969

Date	Number marked limpets remaining		Number emigrant limpets		Median distance travelled (cm)	
	E	C	E	C	E	C
July 30	84	77	0	0	0.0	0.0
August 2	83	74	1	3	20.0	16.7
August 10	66	71	6	4	60.0	50.0
August 15	62	62	16	10	105.5	38.0
September 1	59	58	16	14	160.0	92.1

Table 9

The number of limpets remaining, the number of emigrants and the median distance travelled by emigrants in the experimental (E) and control (C) groups of an experiment designed to measure the response of limpets to reduced food levels. Algae were removed from around the experimental group on June 4 and 5, 1970

Date	Number marked limpets remaining		Number emigrant limpets		Median distance travelled (cm)	
	E	C	E	C	E	C
June 4	93	111	0	0	0.0	0.0
June 5	84	109	6	0	42.5	0.0
June 16	46	90	43	18	54.5	45.0

only slightly higher than that from the control in the 1969 experiment, but the emigrants from the experimental clump travelled a greater median distance than those from the control. In the 1970 experiment, the rate of emigration was higher from the experimental clump, although the median distances travelled by emigrants from both groups were similar.

Availability of space was decreased in an experiment carried out in June, 1969. It was reasoned that by adding limpets to a clump, the space available to the original limpets would be decreased immediately, while there would be no immediate effect on the amount of food present. The number of limpets which emigrated from the clump could, as in the previous experiments, be used as a measure of non-homing, and compared with that from a control clump.

Four similar clumps of limpets were marked with quick-drying paint in June, 1969. Two were designated as experimental groups, and 2 as controls. The number of limpets in each experimental group was doubled by the addition of limpets removed from elsewhere. In addition, the effect of removal and replacement on those limpets that were added to the experimental groups was tested. All the limpets in one experimental and one control clump were removed and immediately replaced in the same site. These were then called the disturbed experimental and disturbed control groups.

The number of original limpets remaining in each clump were recorded the following day, and are presented in Table 10. Few limpets remained in the disturbed groups, while a much higher percentage remained in the undisturbed groups. This indicated that removal and

replacement caused a high proportion of limpets to migrate from their home sites. In addition, each experimental group had fewer limpets remaining than the appropriate control group. This indicated that reduced availability of space may have caused a slight decrease in the proportion of homing limpets.

Table 10

The initial number of limpets in each of four treatment groups in an experiment designed to measure the response of limpets to crowding, and the number that remained in each group after one day. See text for explanation

Group	June 7, 1969	June 8, 1969	
	Initial number of limpets	Number of limpets remaining	Percentage remaining
undisturbed experimental	47	39	82.97
undisturbed control	51	50	98.03
disturbed experimental	52	3	5.76
disturbed control	52	7	13.46

This experiment was repeated in 1970, but was inconclusive for the following reason. Limpets were added to the experimental groups on the morning of a very hot day. Because limpets that are placed on an area do not move about to find shelter sites, and thus are vulnerable to desiccation, all groups of limpets were splashed with seawater at intervals throughout the day. After the following high tide nearly all limpets had moved to new positions, in the control groups as well as in the experimental groups. This made the results inconclusive.

Although these experiments tended to be inconclusive, it appears that sudden decreases in food levels may result in a decreased proportion of homing limpets, and that sudden crowding may have the same effect.

DISCUSSION

The hypothesis that local populations of *Acmaea digitalis* can be regulated by changes in individual homing behaviour was examined in this study. Homing was found to be present in individual *A. digitalis* at Port Renfrew, and there appeared to be a tendency toward two behavioural types with respect to homing. Some limpets returned to a home site consistently, while others were observed to

wander over the study areas. The behaviour seemed to persist during 6 months of observation.

Although homing appeared to be modified as a result of artificial disturbances, it was not conclusively demonstrated that changes in individual behaviour occur as a result of feedback from population density.

There is a striking similarity between the observations of 2 behavioural types in *Acmaea digitalis* and the situation reported by LOMNICKI (1969) in *Helix pomatia*. The cause of 2 types of behaviour in *H. pomatia* remains unexplained, although Lomnicki suggests that behaviour is determined by local density and local resources. KREBS (1970) has shown that levels of aggression in the small rodent *Microtus* change as population levels change; and he suggests that such changes may be important in regulating local densities of *Microtus*. WELLINGTON (1964) has demonstrated that differences among activity levels of members of a moth population contribute to the stability of the population in an unstable, heterogeneous environment. These studies underscore the need to consider variability in the behaviour of individuals within a population.

Further study is needed to determine the basis of observed behaviour patterns in *Acmaea digitalis*, and to evaluate their importance to regulation and stability in population of this species.

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